

Fish diversity and biomass in northern Canadian lakes: northern lakes are more diverse and have greater biomass than expected based on species–energy theory

Pasan Samarasin, Charles K. Minns, Brian J. Shuter, William M. Tonn, and Michael D. Rennie

Abstract: Biodiversity in northern Canada (north of 60°N latitude) is threatened, primarily by increasing resource exploitation and by climate change. Unfortunately, we have relatively limited knowledge of aquatic biodiversity for this region, making it difficult to develop suitable policies to manage these threats. Here we describe, quantify, and test hypotheses related to fish biodiversity and biomass in 37 lakes in a diamond mining district (the Barrenlands) in the Northwest Territories, Canada (64°N, 110°W). To estimate species richness and biomass of fish, we took advantage of exhaustive sampling and monitoring surveys conducted in the region and compared our northern estimates against estimates from southern Canadian lakes. We found that most of the 37 northern lakes contained two to four species, with the largest lake containing eight species. Salmonids dominated this system, with lake trout (*Salvelinus namaycush*) being the dominant species in abundance and biomass. Comparative analysis with similar-sized southern Canadian lakes showed no significant difference in the slopes of species richness versus lake area curves. Surprisingly, total fish biomass distributions for northern, Barrenlands lakes were also similar to southern, Ontario lakes. Overall, our results suggest that Barrenlands lakes are important natural resources of Canada that should be conserved for the future. Under anticipated scenarios of climate change, these lakes may represent important refugia for coldwater fishes (e.g., lake trout) as habitats at the southern edges of their ranges become more limiting.

Résumé : La biodiversité dans le Nord canadien (au nord de 60°N) est menacée, principalement par l'exploitation croissante des ressources et les changements climatiques. Malheureusement, les connaissances sur la biodiversité aquatique de cette région sont assez limitées, ce qui rend difficile l'élaboration de politiques adaptées pour gérer ces menaces. Nous décrivons, quantifions et testons des hypothèses relatives à la diversité et à la biomasse de poissons dans 37 lacs dans un district minier diamantifère (les Barrenlands) des Territoires-du-Nord-Ouest (Canada, 64°N, 110°O). Afin d'estimer la richesse spécifique et la biomasse de poissons, nous avons tiré parti d'études d'échantillonnage et de surveillance exhaustives menées dans la région et comparé nos estimations pour le Nord à des estimations pour des lacs du sud du Canada. Nous avons constaté que la plupart des 37 lacs septentrionaux contenaient de deux à quatre espèces, le plus grand lac en contenant huit. Les salmonidés étaient dominants dans ce système, le touladi (*Salvelinus namaycush*) étant l'espèce dominante en ce qui concerne l'abondance et la biomasse. La comparaison avec des lacs du Canada méridional de dimensions semblables n'a révélé aucune différence significative des pentes des courbes de richesse spécifique en fonction de la superficie des lacs. Étonnamment, les distributions de biomasse totale de poissons dans les lacs septentrionaux des Barrenlands étaient également semblables à celles des lacs méridionaux de l'Ontario. Globalement, nos résultats portent à croire que les lacs des Barrenlands sont d'importantes ressources naturelles du Canada qui devraient être conservées pour l'avenir. Dans les scénarios de changements climatiques anticipés, ces lacs pourraient constituer d'importants refuges pour les poissons d'eau froide (p. ex. le touladi) alors que les habitats aux limites méridionales de leurs aires de répartition deviendront de plus en plus limitants. [Traduit par la Rédaction]

Introduction

Species richness (number of species in a given area) is a fundamental measure of diversity (MacArthur and Wilson 1967), and explaining patterns of diversity is a long-standing goal of ecology. At the global scale, biodiversity and productivity generally decline when moving pole-ward from the equator (Rosenzweig 1995; Kaufman and Willig 1998; Hillebrand 2004; Lewis 2011), a pattern that includes freshwater fishes (Barbour and Brown 1974; Oberdorff et al. 1995). Declines in species diversity at higher latitudes have also been observed at smaller regional scales. For example, Mandrak (1995) found a south-to-north decline in fish species richness for Ontario (Canada) lakes. This finding, if extrapolated,

suggests that northern lakes (defined here as lakes north of 60°N latitude) should have substantially lower species richness relative to lakes in temperate regions. However, difficulties in conducting field work and the general expectation of low fish diversity and productivity in northern regions have resulted in a limited scientific literature on fish in this region compared with more temperate latitudes. For example, Downing and Plante (1993) analyzed fish production from 38 lakes globally, and their dataset included only one lake from northern Canada (Char Lake, Nunavut). These gaps in knowledge may create the perception that the value of northern fishes is low. In turn, increasing resource development in northern Canada could be rationalized by this perception of low biodiversity value, and the harmful altera-

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tion or destruction of fish habitat that often accompanies mining activity could accelerate biodiversity loss in the north.

Here, we investigate fish diversity and biomass of northern lakes in a comparative framework to test hypotheses related to diversity and biomass. Based on species–energy theory (Wright 1983; Currie 1991; Evans et al. 2005) and previously described latitudinal patterns (Mandrak 1995), we expected fish diversity, abundance, and biomass to decrease with decreasing energy availability (i.e., increasing latitude). Energy in a system is typically measured as available solar radiation (Johnson 1994) or using a normalized vegetation index (Storch et al. 2005), depending on the system of interest. Both long-term regional processes such as historical biogeography and climate (Jackson and Harvey 1989; Mandrak 1995; Griffiths 2010), as well as local factors such as lake area and water chemistry (Matuszek and Beggs 1988; Allen et al. 1999), have been shown to explain variation in species richness in temperate regions, and it would be useful to evaluate the relative importance of these factors in northern regions.

Although species richness increases with area (Arrhenius 1921; Gleason 1922) and with energy (Wright 1983; Currie 1991), there appears to be a negative interaction between area and energy (Storch et al. 2005). According to Storch et al. (2005), this interaction causes the slope of the log-transformed species–area relationship to be lower in areas with high energy compared with areas with low energy. That is, the exponent z in the power equation species richness = $c \times \text{Area}^z$ is expected to be smaller for high energy areas compared with low energy areas. This pattern has been found in empirical studies by Lyons and Willig (2002) and Storch et al. (2005). In contrast, the intercept of the log-transformed species–area relationship ($\log[c]$) is expected to be elevated for high energy areas, and the overall relationship for high energy areas is expected to be elevated above the low energy areas. Several explanations have been put forth to explain this phenomenon, including (i) higher rates of speciation in high energy areas, (ii) lower rates of extinction in high energy areas, and (iii) the physiological tolerance hypothesis, which predicts that more species can tolerate warm and wet conditions compared with cold and dry conditions. However there has not been strong support for any particular hypothesis (reviewed by Currie et al. 2004). Nevertheless, based on the observed empirical patterns, we expect the slope of the species–area relationship for southern Canadian lakes to be lower than the slope for northern Canadian lakes, but the intercept is expected to be higher for southern lakes.

Similar to species richness, we expect total fish biomass to decrease with increasing latitude because primary production decreases with increasing latitude (Liu et al. 2002; Lewis 2011), and this reduction in production should exert a bottom-up constraint on consumers such as fish. Downing and Plante (1993) found a positive relationship between annual fish production ($\text{kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$) and mean annual standing fish biomass ($\text{kg}\cdot\text{ha}^{-1}$). Their analysis also showed positive correlations among fish production, temperature, and primary production. Because of these relationships, we predict that the fish biomass of northern lakes will be significantly lower than that of temperate-zone lakes.

We compared fish resources from a northern Canadian region (the Barrenlands; Fig. 1) against similar-sized lakes in southern Canada (primarily Ontario). We predicted that log-transformed species richness would increase at a higher rate with lake area (i.e., have steeper slope) in Barrenlands lakes compared with southern Canadian lakes because of the expected negative interaction between area and energy (Storch et al. 2005). We also predicted that variation in species richness among regions would be largely due to regional factors (historical biogeography and climate) rather than local factors (e.g., lake area) based on previous research on similar aquatic systems (Tonn 1990; Beisner et al. 2006). We also explored the relationships of fish biomass with lake area, mean annual air temperature, mean depth, and num-

ber of species to identify which variables were associated with differences in fish biomass over a broad regional scale. Air temperature was used as a proxy for lake water temperature. Air temperature has been found to be a good predictor of lake water temperature by Sharma et al. (2008) and has been used in models to predict water temperature by others (Matuszek and Shuter 1996; Trumpickas et al. 2009). Finally, we estimated the abundance and biomass of dominant species and described patterns we ascertained with respect to biomass. We expected cold-water species to dominate Barrenlands lakes in numerical abundance and biomass, but because of energetic constraints, we predicted that the biomass of the dominant cold-water species would be lower than that in temperate lakes (Wright 1983).

Materials and methods

Study area and data

The study lakes are located in a diamond mining district in the Barrenlands region (Fig. 1) of the Northwest Territories, Canada, about 330 km northeast of Yellowknife (approximately $64^{\circ}45'N$, $110^{\circ}38'W$). The mining companies operating in this region were required to collect fish and habitat data from local lakes by Fisheries and Oceans Canada (DFO). In some lakes, all the fish were removed and lakes were drained for mine development (hereinafter referred to as fish-out lakes; Tyson et al. 2011), while other lakes were sampled for monitoring purposes (monitored lakes). The data collected included habitat variables such as lake surface area, depth, and water quality; fish data such as species caught, fork length, and mass of individual fish; and fishing effort data such as fished times and gear used. Most lakes had an area of 20–200 ha. Fish were sampled predominantly using gillnets with mesh sizes ranging from 0.7 to 14 cm (0.7, 2.2, 3.8, 5.1, 6.4, 7.6, 10.2, 12.7, and 14 cm), including multimesh nets. Trap nets and angling were used in a few lakes, but this effort was minimal relative to gillnet effort. The database contained 53 lakes or ponds. We used all 53 lakes and ponds for the preliminary regional species richness analysis to document species occurrence in the Barrenlands region (Analysis (a) in Table 1). Because of differences in sampling intensity among lakes, we applied certain inclusion criteria to select lakes that were adequately sampled for subsequent species richness analyses. These criteria are specified in subsequent sections in the Materials and methods and summarized in Table 1. Comparative data for the regional analysis of the relationship between lake area and species richness were obtained from study sites across Canada, as reported in the following sources: Black-Hollow river region, Ontario (Jackson 1988; Jackson and Harvey 1989); Bruce Peninsula, Ontario (Harvey 1981); Manitoulin Islands, Ontario (Harvey 1978); Wawa region, Ontario (Somers 1980; Somers and Harvey 1984); Athabasca region, Alberta (Robinson and Tonn 1989); Vilas County, Wisconsin (Tonn and Magnuson 1982). Fish species richness for secondary watersheds were obtained by pooling tertiary watershed species lists in Chu et al. (2003) according to described secondary watersheds in Minns et al. (2008).

For the comparative analysis of biomass, fish biomass data from lakes were collated from the DFO Barrenlands dataset and the published literature, along with variables such as lake latitude and longitude, lake area, mean depth, and number of species (Appendix A). To estimate the mean annual air temperature for lakes, we used 0.5-degree gridded 1961–1990 temperature data from the CRU TS 2.1 dataset (Mitchell and Jones 2005), available from http://www.ipcc-data.org/obs/cru_ts2_1.html. We obtained lake trout (*Salvelinus namaycush*) biomass data for Canadian lakes through the Ontario Ministry of Natural Resources (Lester 2013). The data are mainly from Ontario lakes, but include lakes from Quebec, Yukon, Alberta, and Saskatchewan. Table 1 summarizes the analyses conducted and the datasets used.

Fig. 1. Location of the study area in Northwest Territories, Canada. Northern Canada (north of 60°N latitude) contains the three Canadian territories: Nunavut, Northwest Territories, and Yukon.



Analyses

All calculations, statistical analyses, and plots were prepared using R version 2.14.2 (R Development Core Team 2012) unless stated otherwise.

Species richness

Species richness for each monitored lake was estimated using EstimateS 8.2.0 (Colwell 2006), which uses sample- or individual-based rarefaction or extrapolation curves to estimate the “actual” species richness. First, we plotted all species richness estimators implemented in the program EstimateS (e.g., Chao, ICE, Jackknife, Michaelis-Menten) as a function of number of sampled individuals in fish-out lakes where we assumed we knew the “actual” species richness because the sampling was exhaustive. We found the species richness estimates from different methods to be very similar for most fish-out lakes, but the Jackknife 1 estimator (Heltshe and Forrester 1983) provided the most accurate estimate of the actual species richness with the least amount of sampling. The Jackknife 1 method estimates total species richness, including species not present in any sample, by incorporating a term for unsampled species in the system, the magnitude of which decreases with increasing sampling effort (Burnham and Overton 1978; Heltshe and Forrester 1983). It provided the best estimate of actual species richness of fish-out lakes when at least 95 individuals were sampled. Therefore, Jackknife 1 was selected to estimate species richness in monitoring lakes that had at least 95 sampled

individuals (Analysis (b) in Table 1). The estimated species richness did not differ from observed species richness in most of the lakes that had at least 95 sampled individuals; in fact, the estimated number of species using the Jackknife 1 method, rounded to the nearest whole number, was identical to the observed species richness in 15 of 18 monitored lakes. For the other three monitored lakes, one had an estimate higher by one species (+1) and two lakes had estimates higher by two species (+2).

We compared the relationships between species richness and lake area among different regions by testing if slopes and intercepts of species–area regression lines were significantly different. Analysis of covariance (ANCOVA) was used to test for heterogeneity in slopes by including the region as the categorical factor (Analysis (c) in Table 1). Lake area (in hectares) and species richness were \log_{10} -transformed to stabilize variance so that the assumption of normality for the residuals was met. Multiple regression analysis was conducted to explain species richness in terms of local (lake area) and regional (secondary watershed species richness) factors (Analysis (d) in Table 1). The best explanatory model was chosen based on corrected Akaike information criteria (AIC_c; Hurvich and Tsai 1989; Anderson and Burnham 2002).

Fish abundance

Fishing effort and catches were calculated from sampling data. For fish-out lakes, we used maximum likelihood and regression-based catch–effort models to estimate total fish abundance. We

Table 1. Summary of main analyses and information on data used for the analysis.

Analysis	Data included in dataset	Data sources
(a) Preliminary regional species richness of Barrenlands lakes	All 53 lakes or ponds in our study area	Barrenlands fish-out database, Fisheries and Oceans Canada
(b) Species richness estimation of Barrenlands monitored lakes	Monitored lakes with >95 individuals sampled	Barrenlands fish-out database, Fisheries and Oceans Canada
(c) ANCOVA of species–area relationship	Barrenlands, four Ontario sites, Alberta, Wisconsin	Barrenlands fish-out database; Harvey 1978; Somers 1980; Harvey 1981; Tonn and Magnuson 1982; Somers and Harvey 1984; Jackson 1988; Jackson and Harvey 1989; Robinson and Tonn 1989
(d) Local versus regional factors explaining species richness	Barrenlands, four Ontario regions, Alberta, Wisconsin	Barrenlands fish-out database; Harvey 1978; Somers 1980; Harvey 1981; Tonn and Magnuson 1982; Somers and Harvey 1984; Jackson 1988; Jackson and Harvey 1989; Robinson and Tonn 1989
(e) Abundance and biomass estimation	Barrenlands lakes >10 ha and >50 fish sampled	Barrenlands fish-out database, Fisheries and Oceans Canada
(f) Comparison of biomass distributions between Barrenlands and Ontario lakes	Barrenlands (monitored and fish-out) and Ontario lakes	Barrenlands fish-out database; Kelso and Johnson 1991
(g) Overall biomass analysis	Barrenlands plus other lake fish biomass data from literature	See Appendix Table A1 for individual sources. Barrenlands fish-out database; Kelso and Johnson 1991; Downing and Plante 1993; Randall et al. 1995; Achleitner et al. 2012
(h) Latitudinal pattern in lake trout biomass	Lake trout biomass data from Barrenlands and other Canadian lakes	Barrenlands fish-out database; N.P. Lester, personal communication

first estimated abundance using standard estimators including the Leslie–Ricker (Leslie and Davis 1939; Ricker 1975), DeLury–Ricker (DeLury 1947; Ricker 1975), and maximum-likelihood (Gould and Pollock 1997) methods. Generally, estimates from different methods were consistent for most lakes. We found that the Leslie–Ricker estimates for fish-out lakes were closest to the total catches obtained from exhaustive sampling in fish-out lakes. Because few of our lakes were sampled with multiple gear types, we needed to modify the Leslie–Ricker method to account for differences in fishing effort resulting from different gear types. We regressed gillnet catch-per-effort (dependent variable) against the cumulative catch from all gears (independent variable) and calculated the initial abundance by dividing the intercept by the negative slope of the regression (i.e., total cumulative catch when catch-per-effort is zero). This is identical to the Leslie–Ricker estimation of abundance, only differing by the use of cumulative catch from all gear types, instead of just one. This method yielded abundance estimates identical to the Leslie–Ricker estimates when all the fishing effort was from one gear type and provided more accurate estimates of total abundance in lakes where multiple gear types were used. Catch-per-effort models assume that enough fish were removed to substantially reduce catch per unit effort over time (Leslie and Davis 1939), which may not be true for monitored lakes where sampling effort was much lower than fish-out lakes. Therefore, we used regression analyses of the fish-out dataset to assess the feasibility of using initial catch per effort (CPE₀) values to estimate total abundance in monitored lakes (Analysis (e) in Table 1).

Biomass and dominance

Fish biomass for each lake was estimated by using the estimated fish abundance and mean mass of fish caught in the lake. To estimate the biomass of individual species, we determined the fraction of fish belonging to each species from catch data. This was multiplied by the total fish abundance to calculate the abundance of the particular species and then multiplied by the mean mass of the species in the lake.

We used the Wilcoxon rank sum test to compare fish biomass distributions from Ontario (Kelso and Johnson 1991) and Barrenlands lakes (Analysis (f) in Table 1). Using a larger dataset (Appendix A) that included lakes from a broad geographic area, we analyzed relation-

ships among fish biomass, lake area, mean depth, mean annual air temperature, and number of species using multiple regression after log₁₀-transformation of fish biomass, lake area, and mean depth (Analysis (g) in Table 1). The model best able to account for observed variation in fish biomass was chosen based on AIC_c. The contributions of the dominant species to total abundance and biomass were quantified, and the relative abundance and biomass of the dominant species were plotted as functions of number of species in the lake. The relationship among lake trout biomass, lake area, and latitude was evaluated using multiple regression after log₁₀-transformations of biomass and lake area (Analysis (h) in Table 1).

Results

Nine fish species were found in our Barrenlands lakes. Lake trout, Arctic grayling (*Thymallus arcticus*), and round whitefish (*Prosopium cylindraceum*) were the most common species, inhabiting at least 32 of the 53 lakes (Fig. 2). Most lakes contained two to four species, but the largest lake (Long Lake) contained eight species. We found significantly more species in fish-out lakes relative to monitored lakes, presumably because of the incomplete sampling of the latter (Wilcoxon rank sum test, $W = 137$, one-tailed $p = 0.01$).

Species–area relationship

Log₁₀(species richness) was linearly related to the log₁₀(lake area) in fish-out lakes (Fig. 3: $R^2 = 0.53$, $F_{[1,8]} = 7.95$, $p = 0.026$), but the strength of the association (judged by the R^2 value) weakened when monitored lakes were included ($R^2 = 0.22$, $F_{[1,25]} = 6.94$, $p = 0.014$). Relationships between species richness and the lake area among different regions showed no significant difference in slopes (ANCOVA: lake area by region interaction, $F_{[1,6]} = 0.98$, $p = 0.436$; Fig. 4). However, there were significant differences in the intercepts ($F_{[1,6]} = 43.12$, $p \ll 0.001$), which ranged from 0.05 for the Barrenlands lakes to 0.64 for Wawa, Ontario. Overall, for a 100 ha lake, mean species richness was 3.7 species in Barrenlands lakes, whereas species richness ranged from 2.6 in Alberta (lowest) to 11.2 in Bruce Peninsula, Ontario (highest).

According to AIC_c, the additive multiple regression model (eq. 1) that included both lake area and secondary watershed species richness was best able to account for the observed variation in

Fig. 2. Occurrence of each fish species in 53 lakes and ponds in the Barrenlands region of Northwest Territories, Canada. ARGR, Arctic grayling; BURB, burbot; CISC, cisco; LKCH, lake chub; LKTR, lake trout; LKWH, lake whitefish; LNSC, longnose sucker; RNWH, round whitefish; SLSC, slimy sculpin.

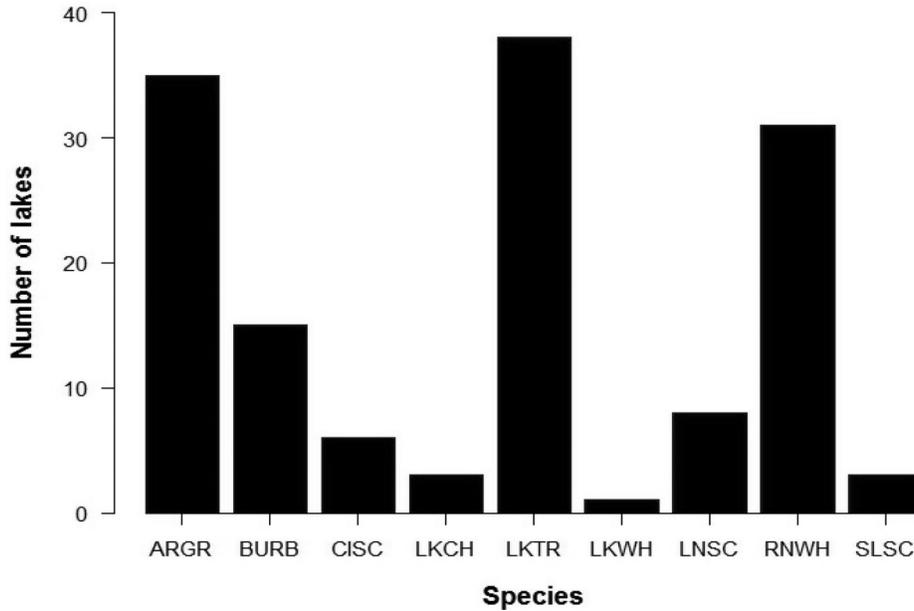
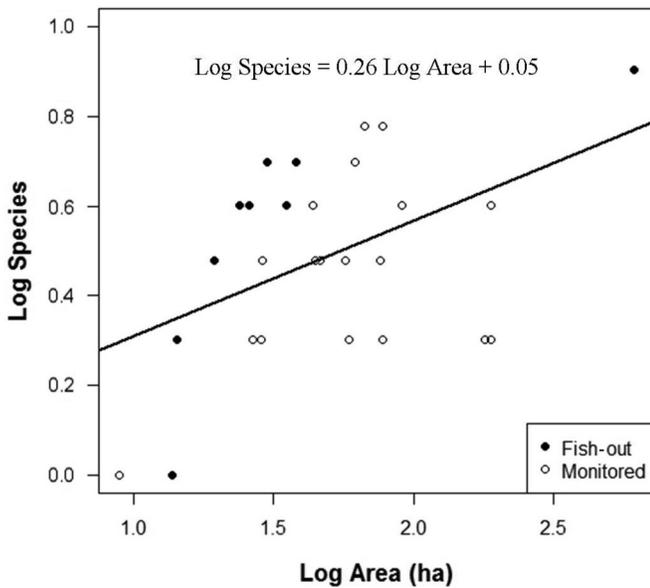


Fig. 3. Relationship between lake area and species richness for Barrenlands lakes. Solid circles are species richness estimates for fish-out lakes, and open circles are species richness estimates for monitored lakes. Regression line shows the overall trend for all lakes.



lake species richness, with secondary watershed species richness accounting for 34% of the observed variance and lake area accounting for 22%.

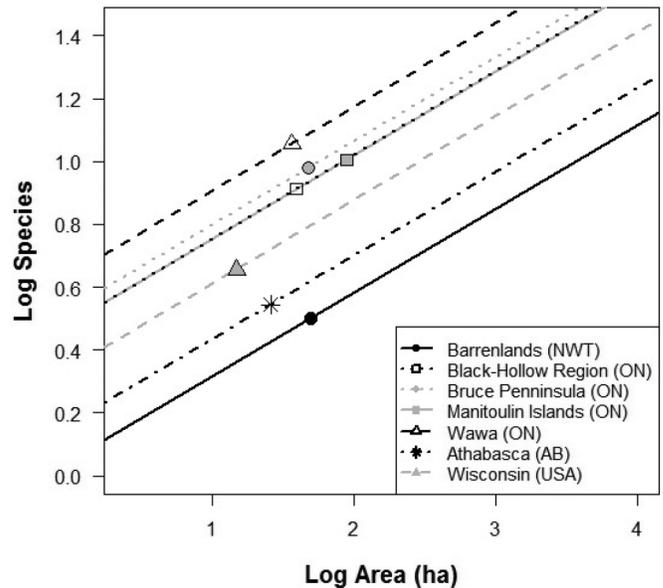
$$(1) \quad \log_{10}(\text{lake species richness}) = -0.73 + 0.24 \log_{10}(\text{lake area}) + 0.62 \log_{10}(\text{secondary watershed species})$$

$$(R^2 = 0.56, F_{[2,279]} = 177.8, p \ll 0.001)$$

Fish abundance, and total biomass

Log₁₀-transformed CPE₀ was linearly related to fish density (in number per hectare; R² = 0.59, p = 0.005) and total fish abundance (R² = 0.79, p < 0.001) for the fish-out lakes. Therefore, we used

Fig. 4. Relationship between species richness and lake area for lakes in different regions in North America. There was no statistical difference in slopes among regions, but intercepts were significantly different (p < 0.001). The common slope was plotted with the region-specific intercept because slopes were not significantly different. Positioning of the symbol indicates the mean lake size for that region. Note that regression lines for Black-Hollow region and Manitoulin Islands coincide.



initial catch per effort of monitored lakes to better estimate the total abundance and biomass of monitored lakes. Total fish biomass in Barrenlands lakes ranged from 0.2 to 25 kg·ha⁻¹, with a median of 10.1 kg·ha⁻¹. Total fish biomass distribution in Barrenlands lakes marginally differed from the small Ontario lakes (Wilcoxon rank sum test, W = 170, p = 0.08; Fig. 5). Our multiple regression analysis using lakes from a broad geographic scale (Appendix A) showed that observed variation in total fish biomass

Fig. 5. Total fish biomass distributions for Barrenlands lakes (light shade) and Ontario lakes (dark shade) on a shared axis. The two distributions were very marginally different ($p = 0.08$; Wilcoxon rank sum test).

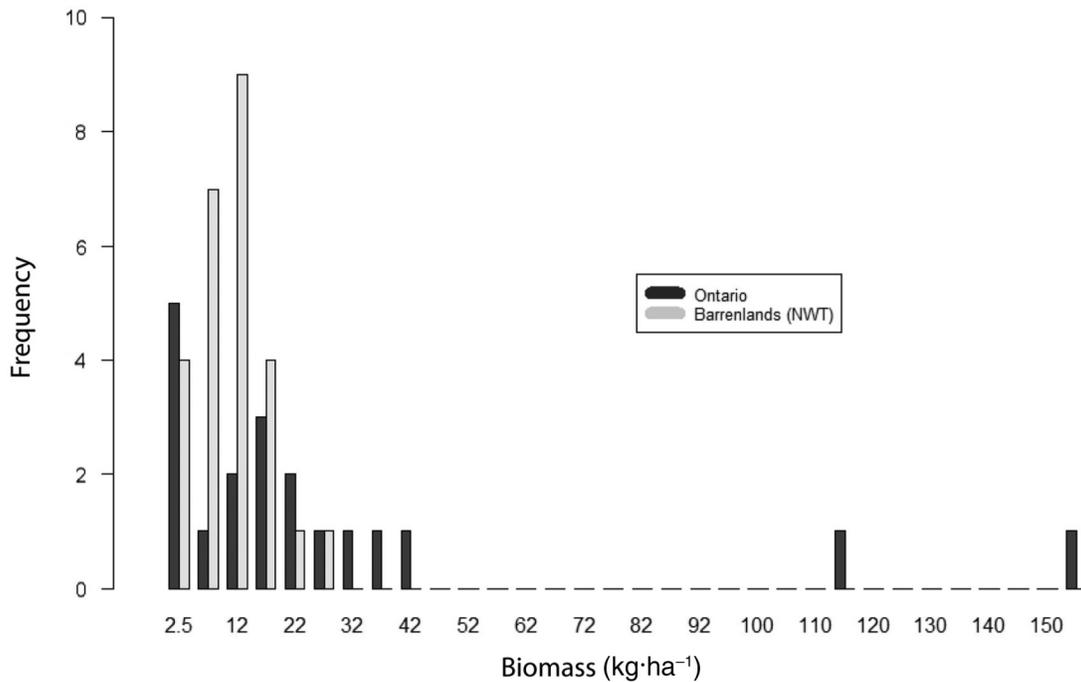
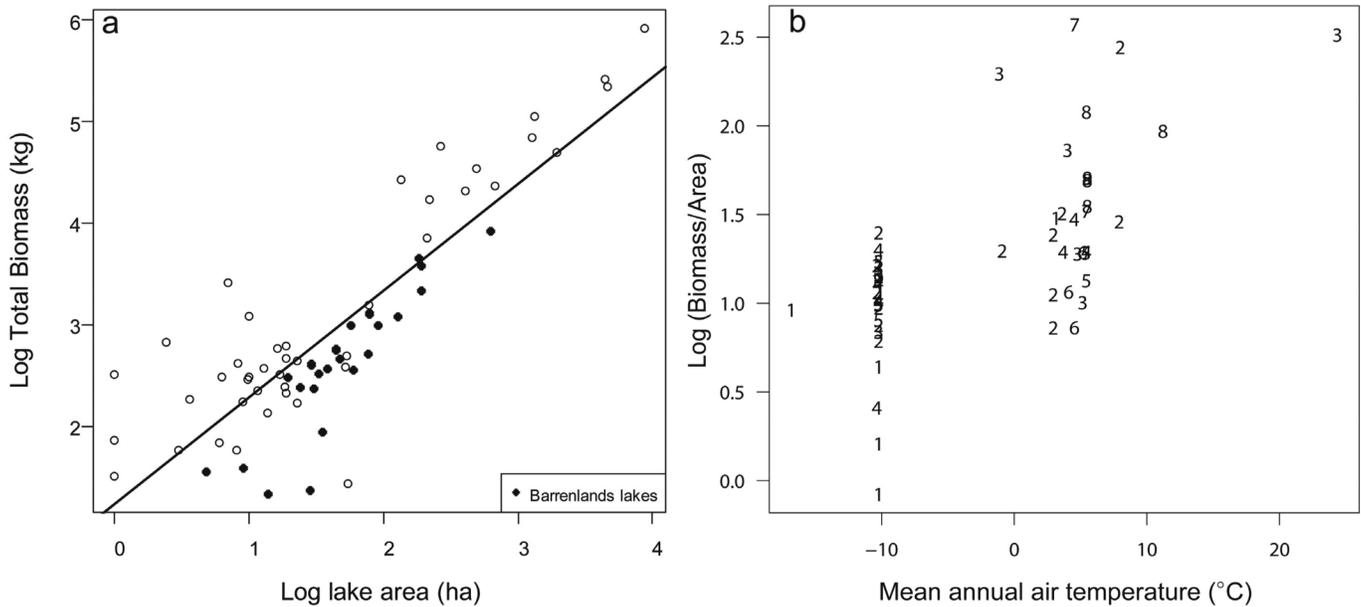


Fig. 6. Relationship between (a) fish biomass and lake area and (b) mean annual air temperature and species richness. (a) Log_{10} -transformed total fish biomass as a function of log_{10} -transformed lake area. Solid circles represent Barrenlands lakes. (b) Log_{10} -transformed biomass per area ($\text{kg}\cdot\text{ha}^{-1}$) as a function of mean annual air temperature, with numerical symbols representing the species richness. Barrenlands lakes are located around -10°C .



was best accounted for by differences in lake area, mean annual air temperature, and number of species in the lake:

$$\log_{10}(\text{biomass}) = 2.49 + 1.04 [\log_{10}(\text{lake area})] + 0.11 (\text{number of species}) + 0.08 (\text{mean annual air temperature})$$

$(R^2 = 0.77, F_{[3,52]} = 59.06, p < 0.001)$

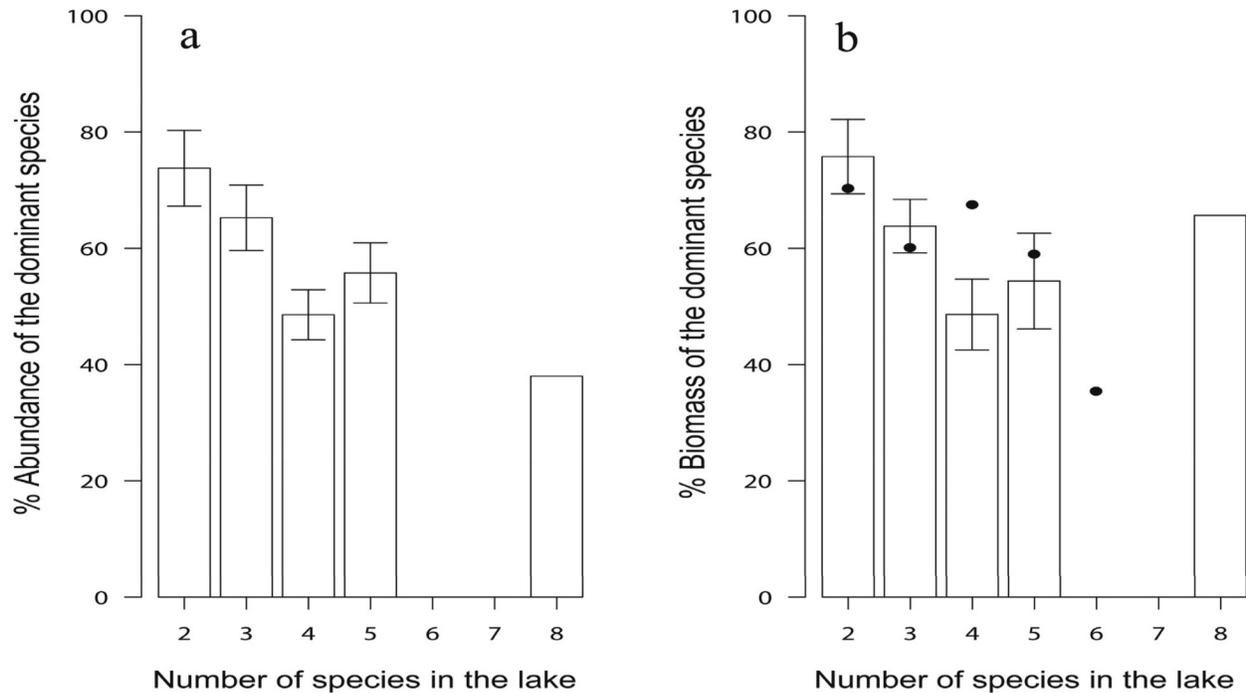
Log-transformed total fish biomass per lake was strongly associated with log_{10} (lake area) (Fig. 6a) and the coefficient (1.04) was

not significantly different from 1. Biomass ($\text{kg}\cdot\text{ha}^{-1}$) was also positively associated with species richness and mean annual air temperature (Fig. 6b).

Dominant species

In terms of abundance, Barrenlands lakes were largely dominated by either round whitefish (14 of 35 lakes) or lake trout (12 of 35 lakes). Lake trout, however, had the greatest biomass in 18 out of 31 lakes. The dominant species contributed a substantial proportion to the total fish abundance and biomass in lakes with

Fig. 7. (a) Mean percent abundance of the dominant species for lakes with more than one species. (b) Mean percent biomass of the dominant species for lakes with more than one species. Solid circles indicate the mean percent biomass of the dominant species from Ontario lakes (calculated from Kelso and Johnson 1991). Error bars represent the standard error of the mean.



more than one species (Fig. 7). Percent abundance of the dominant species declined as species richness increased (Fig. 7a), but still made up 38% of the fish present in the lake with eight species. Similarly, the biomass contribution of the dominant species decreased with increasing species richness, but rarely fell below 50% (Fig. 7b). The dominant species' contribution to total fish biomass in the Barrenlands lakes was similar to that found in Ontario lakes (Fig. 7b).

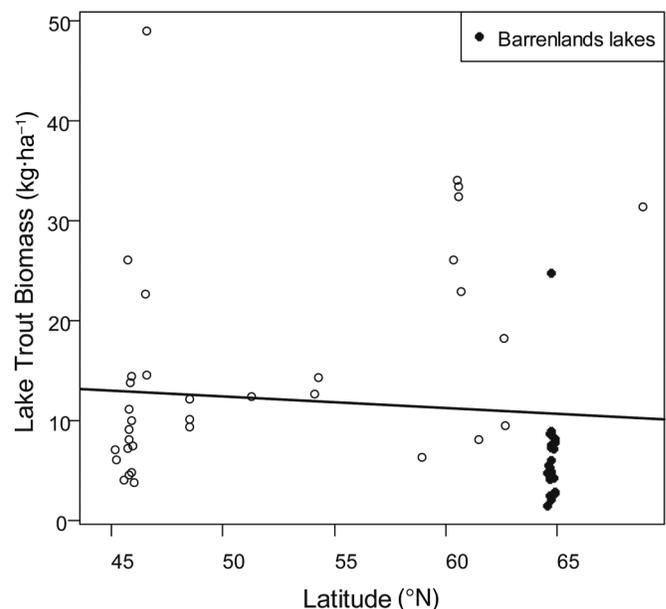
Multiple regression analysis showed no significant effect of latitude on lake trout biomass ($p = 0.75$), but lake area was significant ($p < 0.001$, $R^2 = 0.91$, $F_{[2,54]} = 262.2$). The slope of the regression line (1.13) was significantly different from 1 ($p = 0.029$). Even if biomass was expressed as $\text{kg}\cdot\text{ha}^{-1}$ (i.e., assuming a 1:1 relationship between area and biomass), there was no significant linear relationship between lake trout biomass and latitude (Fig. 8: $R^2 = 0.01$, $F_{[1,55]} = 0.6$, $p = 0.44$).

Discussion

Our results indicate that freshwater fish resources in northern lakes are greater than the general perception and are, in fact, comparable to regions in southern Canada. We found that small lakes in the northern, Barrenlands region contained up to eight species per lake and were dominated by cold-water species such as lake trout, round whitefish, and Arctic grayling. Contrary to expectations from the literature, the slopes of the relationships linking species richness to lake area were not significantly different between northern, Barrenlands lakes and southern, Ontario lakes. Furthermore, our comparative analysis suggests that regional factors are an important determinant of lake fish assemblages.

Contrary to our expectations, we found the Barrenlands fish biomass distribution to be similar to that found in small Ontario lakes. Mandrak (1995) found a gradient in species richness in Ontario, with richness declining from south to north; this led us to expect that Barrenlands lakes, in the far north, would have far fewer species than the lakes in Ontario. However, Mandrak's regional analysis was done at the quadrat level and did not explicitly consider lake area, which often explains considerable variation in

Fig. 8. Lake trout biomass in Canadian lakes. There was no a significant linear relationship between lake trout biomass and latitude ($R^2 = 0.01$, $p = 0.44$). Solid circles represent lake trout biomass in Barrenlands lakes.



species richness at a local scale (e.g., Matuszek and Beggs 1988; Allen et al. 1999). Our comparative analysis, which accounted for lake area, showed that species richness increased with lake area in a similar fashion for both Barrenlands and southern lakes. This result of no significant difference in slopes of species–area curves does not support Storch et al.'s (2005) prediction that low energy areas would have a higher slope than high energy areas and thus questions the generality of a negative interaction between area

and energy with respect to species richness. It is possible that the negative interaction is more apparent when two areas with large differences in energy are contrasted (as in the case for South Africa versus Britain; Storch et al. 2005), but is less apparent when the differences in energy are moderate (Barrenlands versus Ontario).

Although the slope of the species–area relationship was similar across regions, we did find that the northern lakes contained fewer species per unit lake area than southern lakes, as shown by a significantly lower intercept for the Barrenlands species–area curve. The intercept of the species–area curve can be thought of as representing the regional species pool, where high regional richness would increase the intercept because individual lakes are more likely to be colonized by more species. This is consistent with Lyons and Willig's (2002) finding of higher intercept values for the tropics compared with temperate regions. Regional species pools in lower latitudes tend to be larger because of higher energetics and longer biogeographic history; northern Canadian lakes are younger and further from glacial refugia, both of which reduce the number of species available to colonize lakes because of dispersal limitations and less time for speciation to occur (Bernatchez and Wilson 1998; Shafer et al. 2010). For example, Tonn et al. (1990) compared regional fish assemblages in two areas with similar climatic variables (Wisconsin, USA, versus Finland) and attributed most of the higher species richness in Wisconsin lakes to differences in biogeographic histories. Therefore, we infer that the reduced species richness in Barrenlands lakes is largely driven by smaller species pools for this region. This inference is further supported by our analysis that showed a regional factor (i.e., secondary watershed species richness) was a better predictor of lake species richness than a local factor (i.e., lake area). The relative importance of secondary watershed species richness suggests that long-term regional processes, such as historical biogeography and dispersal, play important roles in determining local diversity (Tonn et al. 1990; Beisner et al. 2006; see also Angermeier and Winston 1998; Niu et al. 2012).

Biomass

Biomass is a key ecological variable for quantifying fish resources in a system. Our estimates of fish biomass for the northern lakes ranged from 0.2 to 25 kg·ha⁻¹. Although we expected southern lakes to have higher biomass levels for energetic reasons (Wright 1983; Evans et al. 2005), we found only a marginal difference between the biomass distributions of small Ontario lakes and Barrenlands lakes. Fish biomass estimates for high latitude lakes are rare in the scientific literature (MacCallum and Regier 1984), but Malinen et al.'s (2014) estimates of European whitefish biomass (*Coregonus lavaretus*) in six subarctic Finnish lakes provide a useful comparison for our study because whitefish is dominant in both regions. Their estimates of biomass cover a range (0.5–13.3 kg·ha⁻¹) that is similar to our estimates for the Barrenlands lakes, even though mean annual air temperature of Barrenlands lakes is 5–8 °C lower than these Finnish lakes. This suggests that northern Canadian lakes contain more fish biomass than might be expected based on temperature.

Our analysis of lake fish biomass over a broad geographic range indicated that total biomass increased with lake area, mean annual air temperature, and species richness of the lake. The positive association between species richness and biomass could be due to effects of niche complementarity (Tilman et al. 1997), where more complex systems allow the coexistence of more species (through niche partitioning), and this results in higher total biomass. Similar to Cote et al. (2011), we did not find lake depth to be associated with differences in biomass. This contrasts with previous studies that identified lake depth as an important predictor (Matuszek 1978; Hanson and Leggett 1982). Although the lakes analyzed by Cote et al. (2011) are relatively small, shallow

lakes, our analysis contained lakes that covered a broad range in depths, in addition to the Barrenlands lakes (see Appendix A).

Biomass and production are key ecological variables that help to ascertain the value of fish resources in a system. Although the relationship between fish production and biomass over a broad geographic scale was found to be close to 1:1 by Downing and Plante (1993), we do not expect the 1:1 relationship to hold in northern lakes with cold waters. Northern Canadian lakes, including Barrenlands lakes, are occupied by long-living, slow-growing fish with relatively large size (Johnson 1976; Sparholt 1985). Because production to biomass ratios are inversely related to maximum size and positively related to lake productivity, we expect lower production to biomass ratios in northern Canadian lakes (Randall and Minns 2000; Giacomini et al. 2013). Therefore, although biomass might be relatively similar in northern and southern lakes, we expect overall production to be lower. The observation of low recruitment in Arctic lakes, which are dominated by salmonids such as lake trout and Arctic char (*Salvelinus alpinus*) (Johnson 1994), lends further support to this expectation.

Dominant species

Coldwater species in the Salmonidae family, especially round whitefish and (or) lake trout, dominated Barrenlands lakes. In the northern Nordic region, which has a similar latitude to the Barrenlands, Percidae (European perch, *Perca fluviatilis*), Esocidae (northern pike, *Esox lucius*), together with Salmonidae, are most common (Lehtonen et al. 2008), likely because Nordic lakes are warmer than subarctic North American lakes (Shuter et al. 2012). In contrast, small Ontario lakes are dominated by a combination of both cool-water families, such as Percidae and Catostomidae, and warmwater Centrarchidae (Kelso and Johnson 1991). Only a few species make up most of the biomass in Barrenlands lakes. A relatively small decline in the relative abundance of the dominant species with increasing species richness indicates an uneven distribution of species even in Barrenlands lakes with multiple species. In contrast, we expected the dominant species to contribute less to the total biomass in Ontario lakes because the total number of species is higher; however, we found the contribution of the dominant species to total fish biomass to be very similar to Barrenlands lakes. It appears that only a few species contribute most of the biomass in both areas.

Lake trout

We conducted further analyses of lake trout because of its dominance in the Barrenlands. Although lake trout dominated only 34% of Barrenlands lakes in abundance, it dominated 58% of lakes by biomass. Two sets of information are relevant when predicting a latitudinal cline in lake trout biomass. An extension of the species–energy hypothesis predicts that abundance and biomass will decline with increasing latitude because of decreasing energy availability (Wright 1983; Srivastava and Lawton 1998). In general, cold-water lakes are oligotrophic and have low primary productivity, which limits fish abundance. Based on this information, lake trout biomass should be lower in the northern lakes. However, lake trout are cold-water fish and prefer summer water temperatures of 8–12 °C (Christie and Regier 1988; Magnuson et al. 1990). Based solely on their thermal preference and the amount of habitat available to them at those temperatures, lake trout biomass should be higher in cold-water northern lakes than in warmer southern lakes. Therefore, our finding of no significant latitudinal relationship in lake trout biomass suggests that these two trends balance each other out.

Previous studies in southern Canada (i.e., Ontario) have shown that lake trout is more likely to occur in larger lakes (Ryan and Marshall 1994), and larger lakes contain larger lake trout (Shuter et al. 1998). These observations are consistent with our finding that larger lakes have higher lake trout biomass than smaller lakes (the slope of the regression between lake area and biomass

was significantly higher than 1). Large lakes are typically deeper than small lakes, and this increase in depth would typically add to the additional suitable habitat that is directly associated with increased lake size. Also, in warm summer months, large lakes with greater depths thermally stratify and thus provide hypolimnetic cold-water habitat for lake trout during this season. In winter, deep lakes contain more habitats for lake trout because deep lakes contain a higher proportion of water (in liquid form) compared with small, shallow lakes, which are more susceptible to freezing (Ryan and Marshall 1994).

Future of northern fish

In summary, our findings suggest that northern Canadian lakes support more fish resources than might be expected based on species–energy theory. Many studies predict that with climate change, water temperatures in southern Canadian lakes will exceed optimal temperatures for many fish species, resulting in local extirpations or range contractions (e.g., Schindler 2001; Reist et al. 2006; Eliason et al. 2011). For example, declines of salmonids in southern temperate lakes are predicted because of warming waters (Clews et al. 2010; Pankhurst and King 2010; Blair et al. 2013). As a result, northern lakes represent an important refugia for salmonid fishes that represent substantial commercial, recreational, and aboriginal value, as well as biogeographical reservoirs of biodiversity. Furthermore, northern Canadian lakes, including Barrenlands lakes, are occupied by long-living, slow-growing fish (Johnson 1976; Sparholt 1985), which are more vulnerable to habitat loss (or any other disturbances) than southern fishes because the recovery from a disturbance will likely require a longer period of time.

Fish occupying Barrenlands lakes continue to be threatened by ongoing mineral resource extraction projects in the Barrenlands region (Mackenzie Valley Environmental Impact Review Board 2013). Recent changes to the Canadian Fisheries Act may increase the risk to northern fish populations (Hutchings and Post 2013), but this will depend greatly on how the new Act is enforced. The interpretation of the new Act expressed by Hutchings and Post (2013) suggests that aquatic habitats without a “fishery” (e.g., the Barrenlands lakes) may lose their “right” to protection to speed up mineral extraction projects in northern Canada. Our findings highlight (i) the value of maintaining northern lakes for the future as enclaves of fish biodiversity in Canada and (ii) the need for new research to better understand northern lakes and the fishes they support in the face of ongoing development.

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Appendix A

Appendix Table A1 appears on the following page.

Table A1. Summary of data used for analysis of fish biomass.

Lake	Country	Latitude	Longitude	Lake area (ha)	Total biomass (kg)	Mean annual air temperature (°C)	Fish species richness	Mean depth (m)	Source(s)
Marion	Canada (B.C.)	50.99°N	127.00°W	13	375.7	7.91	2	2.4	Efford 1972
Airstrip*	Canada (N.W.T.)	64.68°N	110.59°W	19.3	306.3	-10.24	3	1.5	This paper
Beartooth†	Canada (N.W.T.)	64.73°N	110.58°W	4.8	36.3	-10.24	2	3.25	This paper
Big Pond†	Canada (N.W.T.)	64.81°N	110.61°W	28.2	23.7	-10.24	1	0.8	This paper
Brandy*	Canada (N.W.T.)	64.72°N	110.74°W	29.9	240.8	-10.24	5	ND	This paper
Counts†	Canada (N.W.T.)	64.65°N	110.29°W	77.5	1 270.4	-10.36	2	1.9	This paper
Cujo†	Canada (N.W.T.)	64.58°N	110.19°W	44.3	591.8	-10.36	3	2.2	This paper
Fay Bay†	Canada (N.W.T.)	64.75°N	110.69°W	46.4	462.2	-10.24	3	2.47	This paper
Grizzly†	Canada (N.W.T.)	64.72°N	110.55°W	58.9	361.9	-10.24	2	14.6	This paper
Horseshoe†	Canada (N.W.T.)	64.87°N	110.54°W	75.7	521.7	-10.24	3	2	This paper
Koala*	Canada (N.W.T.)	64.72°N	110.60°W	38.0	372.3	-10.24	5	5.9	This paper
Kodiak†	Canada (N.W.T.)	64.70°N	110.62°W	90.7	995.9	-10.24	4	2.1	This paper
Logan†	Canada (N.W.T.)	64.87°N	110.77°W	127.2	1 204.1	-10.24	2	5.81	This paper
Long*	Canada (N.W.T.)	64.70°N	110.70°W	614.4	8 411.1	-10.24	8	7.4	This paper
Misery*	Canada (N.W.T.)	64.56°N	110.18°W	13.7	22.1	-10.24	1	7.5	This paper
Moose†	Canada (N.W.T.)	64.68°N	110.64°W	43.6	569.4	-10.24	4	ND	This paper
Nanuq†	Canada (N.W.T.)	64.91°N	110.29°W	189.5	2 188.7	-10.36	2	ND	This paper
Nema†	Canada (N.W.T.)	64.67°N	110.71°W	77.5	1 330.1	-10.24	5	1.9	This paper
Panda*	Canada (N.W.T.)	64.72°N	110.58°W	35.0	90.3	-10.36	4	3.8	This paper
Rene†	Canada (N.W.T.)	64.65°N	110.81°W	32.9	332.1	-10.24	4	ND	This paper
Sable†	Canada (N.W.T.)	64.86°N	110.51°W	8.9	39.1	-10.24	1	6.3	This paper
Slipper†	Canada (N.W.T.)	64.62°N	110.86°W	189.5	3 802.8	-10.24	4	ND	This paper
Two Rock†	Canada (N.W.T.)	64.86°N	110.53°W	28.6	404.2	-10.24	2	3.6	This paper
Ulu†	Canada (N.W.T.)	64.86°N	110.51°W	28.7	415.2	-10.24	3	2.7	This paper
Vulture†	Canada (N.W.T.)	64.75°N	110.54°W	180.2	4 512.8	-10.24	2	ND	This paper
White†	Canada (N.W.T.)	64.70°N	110.76°W	57.2	985.8	-10.24	3	1.9	This paper
Willy*	Canada (N.W.T.)	64.72°N	110.72°W	23.9	248.2	-10.24	4	ND	This paper
Char	Canada (Nun.)	74.71°N	94.90°W	53	487.6	-16.83	1	10.2	MacCallum and Regier 1984
04 Pender	Canada (Ont.)	45.32°N	79.87°W	22.7	442.65	5.44	4	5.3	Kelso and Johnson 1991
14NO Carruthers	Canada (Ont.)	45.37°N	79.87°W	10	1 199	5.44	8	2.7	Kelso and Johnson 1991
20 Cochrane	Canada (Ont.)	45.32°N	79.94°W	18.9	625.59	5.44	7	3.2	Kelso and Johnson 1991
33 Lane	Canada (Ont.)	45.35°N	79.93°W	18.5	247.9	5.44	5	3.1	Kelso and Johnson 1991
A1 Orange	Canada (Ont.)	45.60°N	79.90°W	9.8	292.04	4.53	4	2.1	Kelso and Johnson 1991
Big Turkey	Canada (Ont.)	47.05°N	84.42°W	52	379.6	2.94	2	12.2	Kelso 1988
C1 Crow	Canada (Ont.)	45.78°N	80.23°W	11.5	223.1	5.16	6	2.6	Kelso and Johnson 1991
K12 Raven	Canada (Ont.)	45.53°N	80.20°W	13.6	137.36	5.16	3	3.2	Kelso and Johnson 1991
K25 Turbid	Canada (Ont.)	46.12°N	81.19°W	17	323	4.78	3	2.1	Kelso and Johnson 1991
Little Turkey	Canada (Ont.)	47.04°N	84.41°W	19	212.8	2.94	2	6	Kelso 1988
Lonesome	Canada (Ont.)	45.35°N	75.05°W	3.6	182.88	5.50	8	2.8	Fraser 1981
Long Pond	Canada (Ont.)	42.58°N	80.42°W	2.4	666.72	7.98	22	ND	Mahon and Balon 1977
Pine	Canada (Ont.)	45.35°N	75.05°W	16.4	577.28	5.50	8	4.6	Fraser 1981
Red deer	Canada (Ont.)	45.53°N	79.14°W	6	69.6	4.10	6	3.7	Chadwick 1976
Redpine	Canada (Ont.)	45.35°N	75.05°W	8.3	420.81	5.50	9	2.4	Fraser 1981
Sawlog	Canada (Ont.)	45.35°N	75.05°W	6.3	310.59	5.50	8	4.3	Fraser 1981
Wishart	Canada (Ont.)	47.04°N	84.40°W	19	463.6	2.94	2	2.2	Kelso 1988; Downing et al. 1990
Achensee	Austria	47.46°N	11.71°E	680	22 984	4.38	ND	67	Achleitner et al. 2012
Altaussee See	Austria	47.64°N	13.78°E	210	7 098	5.68	ND	35	Achleitner et al. 2012
Attersee	Austria	47.88°N	13.55°E	4 620	216 678	5.68	ND	84	Achleitner et al. 2012
Faaker See	Austria	46.58°N	13.93°E	220	17 226	4.43	ND	16	Achleitner et al. 2012
Fuschlsee	Austria	47.80°N	13.28°E	265	56 445	5.97	ND	37	Achleitner et al. 2012
Grundlsee	Austria	47.63°N	13.86°E	410	20 459	5.68	ND	32	Achleitner et al. 2012
Millstatter	Austria	46.80°N	13.57°E	1 328	113 411.2	4.43	ND	88.6	Achleitner et al. 2012
Obertrumer	Austria	47.96°N	13.09°E	488	34 355.2	5.97	ND	17	Achleitner et al. 2012
Toplitzsee	Austria	47.64°N	13.93°E	54	27	5.68	ND	62	Achleitner et al. 2012
Wolfgangsee	Austria	47.73°N	13.44°E	1 284	69 464.4	5.97	ND	52	Achleitner et al. 2012
Worthersee	Austria	46.62°N	14.16°E	1 939	50 026.2	7.13	ND	42	Achleitner et al. 2012
La Luisa	Cuba	22.72°N	82.13°W	1	325.7	24.37	3	1.4	Hoiakf 1970
Alinen Mustajarvi	Finland	61.56°N	22.04°E	1	73	4.03	3	3	Rask and Arvola 1985
Horkkajarvi	Finland	61.21°N	25.16°E	1	32.2	3.60	2	7	Rask and Arvola 1985; Arvola 1983
Iso Mustajarvi	Finland	62.12°N	23.47°E	3	58.5	3.69	4	ND	Lappalainen et al. 1988
Nakuru	Kenya	0.36°S	36.10°E	4 400	261 360	15.25	ND	2.3	Vareschi and Jacobs 1984, 1985; Plante 1987

Table A1 (concluded).

Lake	Country	Latitude	Longitude	Lake area (ha)	Total biomass (kg)	Mean annual air temperature (°C)	Fish species richness	Mean depth (m)	Source(s)
Ovre Heimdalsvatn	Norway	61.42°N	8.87°E	78	1 544.4	-0.92	2	4.7	Kloster 1987; Lien 1978, 1981; Tangen and Bretum 1978
Dalnee	Russia	47.50°N	47.06°E	136	26 792	-1.12	3	31.5	Krogus et al. 1972
Demenets	Russia	56.64°N	29.69°E	7	2 605.4	4.55	7	3.3	Gulin and Rudenko 1973
Botjarn	Sweden	60.27°N	15.07°E	10	303	3.14	1	3.3	Nyberg 1979; Ramberg 1976
Coleback Hills	USA	45.02°N	67.21°W	9	172.8	5.42	5	ND	Rupp and DeRoche 1965
Hills	USA	44.56°N	70.18°W	8	58.4	ND	5	ND	Rupp and DeRoche 1965
Shagg	USA	44.42°N	70.53°W	23	167.9	4.54	6	ND	Rupp and DeRoche 1965
Washington	USA	47.61°N	122.26°W	8 760	818 184	11.21	8	33	Edmondson 1977; Eggers et al. 1978

Note: B.C., British Columbia; N.W.T., Northwest Territories; Nun., Nunavut; Ont., Ontario; ND, no data.

*Fish-out lake from Barrenlands.

†Monitored lake from Barrenlands.